Observations of deep-sea fishes and mobile scavengers from the abyssal DISCOL experimental mining area

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Abstract

Industrial interest in deep-sea mineral extraction began decades ago and today it is at an all-time high, accelerated by global demand for metals. Several seafloor ecosystem disturbance experiments began in the 1970's, including the DISturbance and reCOLonization experiment (DISCOL) conducted in the Peru Basin in 1989. A large seafloor disturbance was created by repeatedly ploughing the seafloor over an area of ~10.8 km^2. Though a number of studies in abyssal mining regions have evaluated megafaunal biodiversity and ecosystem responses, few have included quantitative and detailed data on fishes or scavengers despite their ecological importance as top predators. We used towed camera transects (1989-1996, 2015) and baited camera data (1989-1992) to evaluate the fish community at the DISCOL site. The abyssal fish community included 16 taxa and was dominated by *Ipnops meadi*. Fish density was lower in ploughed habitat at 6 months and 3 years following disturbance but thereafter increased over time. Twenty-six years post disturbance there were no differences in overall total fish densities

32 between reference and experimental areas, but the dominant fish, *I. meadi*, still exhibited much

33 lower densities in ploughed habitat, likely avoiding these areas and suggesting that the fish

34 community remains affected after decades. At the scale of industrial mining, these results could

35 translate to population level effects. . The scavenging community was dominated by eelpouts

36 (*Pachycara* spp), hermit crabs (*Probeebei mirabilis*) and shrimp. The large contribution of

37 hermit crabs appears unique amongst abyssal scavenger studies worldwide. The abyssal fish

38 community at DISCOL was similar to that in the more northerly Clarion Clipperton Zone,

39 though some species have only been observed at DISCOL thus far. Also, further species level

40 identifications are required to refine this assessment. Additional studies across the polymetallic

41 nodule provinces of the Pacific are required to further evaluate the environmental drivers of fish

42 density, diversity and species biogeographies. This information will be important for the

43 development of appropriate management plans aimed at minimizing human impact from deep-

44 sea mining.

45

1. Introduction

The world's oceans are becoming increasingly exploited for their resources, and anthropogenic effects now reach the farthest corners and depths of ocean ecosystems (Ramirez-Llodra et al., 2011). New uses of our oceans are emerging. Industrial interest in deep-sea mineral extraction is at an all-time high, accelerated by global demand for minerals such as cobalt, zinc, copper, nickel, and rare-earth elements, which are enriched in seamount crusts as well as manganese nodules and deposited at hydrothermal vents. Currently, the International Seabed Authority has granted 29 exploration contracts to companies to explore for metals and rare-earth minerals in areas totaling >1,200,000 km^2 of seafloor in the Pacific, Atlantic, and Indian Oceans (www.isa.org.jm). Though the current intensity of commercial interest combined with technological innovations will soon lead to exploitation, this idea has a long history. Thus several seafloor ecosystem disturbance experiments were performed beginning in the 1970's (reviewed in Jones et al., 2017).

One of these, the DISturbance and reCOLonization experiment (DISCOL) was conducted in the Peru Basin in 1989. A large experimental seafloor disturbance was created by repeatedly ploughing the seafloor. Biological surveys were conducted prior to the disturbance and several times thereafter to monitor seafloor ecosystem recovery (Thiel et al., 2001). Studies of the site seven years after disturbance showed only partial recovery (Thiel et al., 2001;Bluhm, 2001). Similar studies carried out in the north Pacific have also given indications that seafloor communities have not recovered or only partially recovered in periods of 26-37 years following disturbance (Miljutin et al., 2011;Jones et al., 2017;Gollner et al., 2017). This is not surprising given low rates of recruitment and growth common in these ecosystems, and the removal of the hard substrate upon which a large portion of the fauna depends (Amon et al., 2016;Vanreusel et al., 2016;Purser et al., 2017).

Though a number of studies in abyssal mining regions have evaluated megafaunal biodiversity and ecosystem responses, few have included quantitative and detailed data on fishes or scavengers (Leitner et al., 2017). However, many fishes are top predators that can have important influences on communities and ecosystems (Estes et al., 2011;Drazen and Sutton, 2017). Though fishes are mobile and may not suffer immediate mortality from mining, they will be affected by the large sediment plumes created (Oebius et al., 2001) and by the loss of foraging habitat or prey resources. Thus, they may suffer regionally from local mining activities. Also,

77 top predators can bioaccumulate metals and other contaminants (Chouvelon et al., 2012;Choy et

78 al., 2009;Bonito et al., 2016) that may be released from the activities of mining. Thus, it is

79 important to characterize the fish community in regions that will likely experience mining in the

80 near future and to begin constructing species ranges and community biogeographies, so that

81 scientists and managers can evaluate potential mining impacts and appropriately locate protected

82 no-mining zones (Wedding et al., 2013).

83   In 2015 a survey was performed of the DISCOL area using photo and video transecting

84 techniques in a similar manner to the historical surveys of the area conducted into the late 1990s.

85 In addition, archived analogue baited camera images collected shortly after the 1989 disturbance

86 (1989-1992) were digitized and analyzed for fishes and other mobile scavengers, some of which

87 may avoid transecting vehicles (Trenkel et al., 2004;Colton and Swearer, 2010). Our goal was to

88 a) describe the fish and scavenger community in the DISCOL region in detail for the first time,

89 b) evaluate the fish community response to disturbance and potential recovery, and c) compare

90 the fish and scavenger community to that observed to the north of the equator in the Clarion

91 Clipperton Zone (CCZ). The majority of abyssal mining exploration licenses have been thus far

92 granted in the CCZ, and this is where initial pilot mining activities are likely to commence.

93

94 **2. Methods**

95   In 1989 a ~10.8 km² circular region of the Peru basin in the Pacific, the DISCOL

96 experimental area (the DEA), was artificially ploughed, in an effort to simulate the effects of

97 deep-sea mining (Thiel et al., 2001). The study site (7º 04.4' S, 88º 27.60' W) ranges in depth

98 from 4120-4200 m. Sediments are fine grained clays overlain with heterogeneous cover of

99 manganese nodules, sometimes in high density. The plough-harrow device was 8 m wide and

100 when deployed, overturned the first 10-15cm of seafloor sediment, ploughing the nodules into

101 the seafloor and removing this hard substrate from the sediment / water interface. The plough

102 was towed in 78 radial transects through the disturbance area with ˜20% of the seafloor directly

103 disturbed by the plough. The most central region of the DEA was the most highly disturbed area

104 crosscut by the majority of plough tows (Fig. 1; Foell et al., 1992).

105   In 2015 the DISCOL site was revisited and sampled twice (RV Sonne cruises SO242-1

106 and 2). The initial cruise was conducted in the summer and primarily conducted detailed

107 acoustic and image-based mapping of the plough tracks using Autonomous Underwater Vehicles

108   and ship-based sensors. This initial cruise also towed an epibenthic sled (EBS) several times

109   across the seafloor, removing the top 20 cm of seafloor in trenches of ~2m x 500 m. These sled

110   deployments were conducted to more accurately simulate the upper sediment removal envisioned

111   as a likely consequence of mining. The second of these cruises focused on the detailed

112   photographic study of the historic and recent disturbances mapped during the first cruise.

113   For investigation of megafauna, including fishes, the Alfred Wegner Institute (AWI)

114   OFOS LAUNCHER towed camera system was used to conduct photographic transects of the

115   seafloor. The OFOS LAUNCHER is identical to the OFOBS system described in Purser et al.

116   (2018), with the exceptions that the OFOS was not equipped with INS, side scan or forward

117   facing sonar systems. OFOS was flown at a height of ~1.7m above the seafloor and used a 23

118   megapixel downward looking still camera (iSiTEC, CANON EOS 5D Mark III) to take images

119   every 15 seconds, each of which also captured the laser points projected by a tri-laser (50 cm

120   spacing) sizing device (iSiTEC, custom built). Ship speed was maintained at 0.2-0.4 knots.

121   Given the high heterogeneity of the seafloor area studied, each image was manually

122   assessed to represent one of a range of disturbance categories. These were 1) 'Reference' areas,

123   not directly within the target circle of seafloor ploughed in 1989 (DEA), 2) 'Undisturbed' areas

124   within the central DEA circle, but not actually impacted by the plough harrow directly, 3)

125   'Transition' images, within which both the edge of a plough track was visible as well as

126   surrounding seafloor, 4) 'Ploughed' images within which only ploughed seafloor was visible and

127   5) 'EBS' areas, disturbed a month prior to SO242-2 by the towed epibenthic sled deployed by

128   SO242-1. These five disturbance categories represent increasing levels of physical disturbance.

129   Image area captured within each image was determined by measuring the spacing of the

130   laser points in a subset of 3663 images using the PAPARA(ZZ)I software application (Marcon

131   and Purser, 2017). The image area of all remaining images was calculated from the camera

132   altitude (distance to seafloor) using a second order polynomial regression of the laser-based

133   measurements. The average seafloor image area was 5.71 ± 3.44 m^2 (interquartile range 4.45-

134   6.25 m^2). In some instances, the camera was manually triggered to capture images of fishes that

135   would have been missed in between timed images, or to capture a fish at a more suitable angle

136   for identification. Images were manually annotated for fishes using a variety of published keys.

137   For data on octopi see Purser et al., (2017) and for all invertebrates and benthic fauna see

138   Marcon et al. submitted. Fish density was estimated by dividing the number of fish viewed in

139 regular timed images by the area photographed. Manually triggered images were not included in

140 density estimates as these would present a positive bias towards images with fish in them.

141 Diversity was evaluated using rarefaction curves (on all images, timed and manually triggered,

142 because this approach only requires positive occurrences) to enable comparisons between habitat

143 types that were not sampled at the same intensity.

144 OFOS transects often crossed several habitat types, so for fish density estimates, the

145 images from each transect were divided into habitat type transects. For some habitat transects,

146 there were very few images collected. We eliminated those habitat transects which were so

147 small that they were unlikely to contain at least one fish. We based this assessment on the mean

148 density of all habitat transects (both large and small) of 30.6 fish ha^{-1}, translating to a threshold

149 sample area of 330 m^2. If used in the analysis, these small habitat transects would either bias the

150 results towards zero estimates if no fish were present in the small image set, or towards

151 incorrectly high estimates if a few fish happened to be present. Fish density was compared

152 between habitat types using a permutational ANOVA on a Euclidean distance matrix to account

153 for uneven sample sizes and non-normal data distribution.

154 Baited cameras are now a widely used tool to census marine fishes (Bailey et al., 2007)

155 because they can attract often sparsely distributed animals to within the census view, including

156 some that might avoid active camera survey tools. Thus, for fully describing diversity and

157 species abundances within a regional fish assemblage, they are indispensable. However, in

158 contrast to transect methods, they are more difficult to use for estimations of accurate animal

159 densities (Priede and Merrett, 1998;Yeh and Drazen, 2011).

160 During the first post disturbance cruise in 1989 and three years later in 1992 (Sonne

161 cruises 61 and 77), free fall baited cameras (freefall baited observing systems - FBOS) were

162 deployed (Brandt et al., 2004). These utilized a Benthos 35mm survey camera and strobe. Bait

163 (a single 500-1000g Carangid or Lutjanid) was attached to a rod or placed in a small clear plastic

164 tube ~1m from the camera, resting on the seafloor. Oblique images of ~1.7m^2 of the seafloor

165 were taken every 2 to 5.5 min for ~24 to 55 hours, averaging 725±43 images per deployment.

166 Animals were counted in each image. Metrics extracted from the imagery include the maximum

167 number of each taxon visible in any one image over the camera deployment (MaxN), the time of

168 first arrival for each taxon (T_{arr}), and the proportion of images in which a taxon was present for a

169 camera deployment (Yeh and Drazen, 2011;Linley et al., 2017;Leitner et al., 2017). Only

170   species that were clearly attracted to the bait were enumerated. This eliminated species that were

171   photographed as they were simply drifting or crawling through the field of view, such as medusa

172   and holothurians. Further, many small amphipods were often present at the bait but could not be

173   reliably counted and so are not included. Deployments in 1989 were made within both the

174   reference and disturbance areas, and a PERMANOVA test was used to compare community

175   compositions on a Bray-Curtis similarity matrix based on square root transformed MaxN data.

176

177   **3. Results**

178   3.1 Photographic transects

179   20 OFOS transects were performed resulting in 46 habitat transects (Fig. 1). From these a

180   total of 16733 images were examined with 306 fishes observed in 300 images (Table 1). Fishes

181   were represented by 14 taxa (not including the category "unidentified fishes"; Fig. 2). Several

182   groups were distinct but could not be identified to species whereas others were only identifiable

183   to genus or family. The most common species observed was the benthic *Ipnops* cf *meadi*

184   representing 61% of the fish observations. The Ophidiids were the most speciose family

185   observed with 6 operational taxonomic units (OTU), some of which were distinct but could not

186   be identified conclusively.

187   Across the five different habitat types, sampling effort was very uneven. Within the full

188   data set, images taken of reference area habitat and in unploughed habitat within the

189   experimental area were most abundant (Table 1). Seafloor images showing the disturbed habitat

190   types (transient, ploughed and epibenthic sled (EBS) tracks) were less numerous. For all the data

191   combined, as well as for the unploughed habitat type alone, rarefaction curves suggested

192   adequate sampling as an asymptote was beginning to be reached in both cases (Fig. 3).

193   However, within the other habitat types, rarefaction curves suggested more sampling was

194   required to fully capture the fish diversity. Thus, the use of estimated species richness was

195   needed for diversity comparisons. Interestingly, the disturbed habitat types had higher rarified

196   diversity (ES 26) than the reference area or neighboring unploughed habitat (Fig. 3).

197   Fish densities were highly variable. Across all habitat transects, seafloor areas imaged

198   ranged from 355 to 7798 m^2 and fish density ranged from 0 to 71.4 fish ha^{-1}. Average fish

199   density was 30.2 ± 18.2 fish ha^{-1} (Fig. 4). Across the habitat types, density did not vary

200   significantly (PERMANOVA, p>0.05). The density of the most common fish, *I. meadi*, could

201   also be estimated and ranged from 0 to 68 fish ha^{-1}, averaging 18.4 ± 17.5 fish ha^{-1} across all

202   habitat types (Fig. 4). Its density was significantly lower in the ploughed habitat type compared

203   to undisturbed and reference habitats. Only a single *I. meadi* was found in the EBS habitat type

204   (Table 1), but this individual did not occur in a habitat transect of sufficient length for density

205   estimation. *Ipnops meadi* density in the two habitat transects available for analysis was zero.

206   Since the time of initial disturbance fish density in the DEA varied. No fish were

207   observed 6 months post disturbance, then fish density increased at year 3 and had returned to

208   pre-disturbance density levels after 7 years (Fig. 5; Bluhm 2001). At this time, ophiuroids,

209   holothurians, fish and hermit crabs were observed in the plough tracks. We examined this data

210   (1989-1996) and the 2015 data for the reference, ploughed and unploughed habitat types using a

211   two factor PERMANOVA. Habitat type and time were significant predictors of fish density with

212   lower fish densities in the ploughed habitat ($p<0.01$; Supplementary Table 1). Also, the

213   differences in the densities of fish across the three habitat types changed significantly with time

214   since the disturbance (habitat x time, $p<0.05$). Fish density in the ploughed habitat was

215   significantly ($p<0.05$) lower than the other habitat types right after the disturbance, marginally

216   lower at 6 months post disturbance ($p=0.057$), and significantly lower at 3 years post

217   disturbance. At 7 years the undisturbed habitat type in the DEA had higher fish density than the

218   reference area. At 26 years, as already mentioned, there was no difference between habitats. Fish

219   densities were similar to levels found in the undisturbed habitats and the reference area at 3 years

220   post disturbance but higher than other times (Fig. 5). It was not possible to evaluate the times

221   series data for *I. meadi* as Bluhm (2001) did not publish species specific results.

222

223   3.2 Baited camera observations

224   Six baited camera deployments were conducted, 5 in 1989 and 1 in 1992 (Table 2). Six

225   taxa of fishes were identified (Fig. 6). The most abundant (MaxN) taxon in the deployments was

226   the eelpout *Pachycara nazca*. This species occurred in all 6 deployments, reached a MaxN of 9

227   in two of the deployments and on average was present in 55% of the images. Individuals of the

228   rattail *Coryphaenoides* sp. were either *C. armatus* or *C. yaquinae,* or both were present but, we

229   could not differentiate them in the photographs. This taxon was present in all of the deployments

230   but was observed on average in only 2.1% of images, and MaxN was never more than 2. Several

231 ophidiids and a synaphobranchid eel were also observed. Ophidiids were generally rare and seen

232 infrequently though *Bassozetus nasus* did generally persist at the bait when observed.

233   The baited camera also attracted 9 taxa of invertebrates (Table 2). The small shrimp

234 *Hymenopeneus nereus* was present in all of the deployments in relatively large numbers (average

235 MaxN = 9), with up to 15 visible at one time and was present on average in 63% of the images.

236 The hermit crab *Probeebei mirabilis*, was also observed in every deployment but in varying

237 numbers (from 1 to 9) and in 29% of the images. Penaeid shrimp were also observed in every

238 deployment and were the third most abundant and common scavenging species. Two species

239 were identified, *Cerataspis monstrosus* (identified as *Plesiopeneus armatus* in earlier papers;

240 Leitner et al 2017) and *Benthiscymus* sp. Frequently, these could not be distinguished as they

241 differ in the shape of the antennal scale and rostrum which were not always clearly visible.

242 Large Munnopsid isopods were seen in all but one deployment but did not remain in the field of

243 view for long. Ophiuroids were not abundant or common, being observed in three deployments

244 as single individuals, but they stayed in the field of view for a long time (high persistence

245 values).

246   Two of the camera deployments in 1989 were made in the disturbance area 6 months post

247 event. In one of these deployments there was no obvious sign of disturbance in the limited field

248 of view. In the other, a plough harrow track was clearly visible (FBOS006; Table 2). Low

249 numbers of the benthic eelpout, *P. nazca*, were observed during this deployment. This

250 deployment also had the lowest numbers of the benthic shrimp, *H. nereus*. However, the

251 community composition did not vary significantly between the 1989 deployments inside the

252 disturbance experiment area and reference areas (PERMANOVA, $p > 0.05$). Further, the times of

253 first arrival of the scavengers was variable between deployments and not consistently longer at

254 the disturbance area except for *B. iris* (Supplementary Table 2).

255   Overall, the diversity observed with the small number of camera deployments was fairly

256 uniform, as evident from the plateau reached in both rarefaction and species accumulation curves

257 (Fig. 7). This was the case for all scavengers and for the fishes alone. The baited cameras

258 observed fewer taxa of fishes compared to the photo transects (Table 1, 2). Many of the fishes

259 observed in the photo transects included less mobile benthic species such as members of the

260 Ipnopidae, Bathysauridae and numerous unidentified ophidiids. However, the baited camera

261 deployments identified two fish species that were not observed in the photo transects, *Barathrites*

262 *iris* and a Synaphobranchid eel, both mobile scavengers.

263

264 **4. Discussion**

265 *4.1 A description of the fish and scavenging community and relationship to past DISCOL studies*

266   We present some of the first detailed fish assemblage information for the abyssal eastern

267 Pacific. Earlier studies at the DISCOL site presented limited fish assemblage results from the

268 first few years of the experiment and report finding 8 fish taxa with *Ipnops* sp. being the most

269 abundant (Bluhm, 1994). All of the taxa that were observed in these initial investigations were

270 also present in our 2015 survey results, with the exception of *Halosaurus* sp. Moreover, we

271 observed 6 additional taxa in 2015, and together with analysis of the 1989-1992 baited camera

272 deployments, we have observed a total of 16 taxa. Interestingly, the earlier camera transect

273 surveys flew the camera system higher off the bottom (3-3.5m vs 1.7m) which is perhaps more

274 appropriate for the survey of larger, mobile fishes. Advances in photographic identification of

275 abyssal fishes across the Pacific and improvements in photographic quality have resulted in the

276 greater detail in the present analysis.

277   The baited camera deployments provided additional information on the DISCOL fish

278 community and also provided data on scavenging invertebrate fauna. Past taxonomic works

279 have used trapped specimens to document the presence of the eelpouts *P. nasca* and *P. bulbiceps*

280 (Anderson and Bluhm, 1997) and the ophidiid *B. iris* (specimen deposited at the Senckenberg

281 Museum). The physical specimens provide some vouchers for taxa that were identified from

282 photographs. Two taxonomic studies used the baited camera imagery to tentatively identify the

283 ophidiid *Bassozetus nasus* (Nielsen and Merrett, 2000) and large Munnopsid isopods which were

284 thought to belong to the genus *Paropsurus* (Brandt et al., 2004). Bluhm et al (1995) briefly states

285 that *P. mirabilis* and ophiuroids were commonly seen in the baited camera photos, but these

286 results were not given in any detail. We show the eelpouts, the shrimp *H. nereus*, and hermit

287 crabs are indeed common and regular bait attending fauna at this site (see below for comparisons

288 to other abyssal regions).

289

290 *4.2 Evaluation of the fish community response to disturbance and potential recovery*

291   Our results, 26 years post disturbance, when compared to earlier sampling, provide some

292   insight into the recovery potential of the fish fauna. The striking result found by Bluhm (2001)

293   was that no fishes were observed in the disturbance area within 6 months of the disturbance;

294   however, we show the presence of fish and scavenging invertebrates at this time from baited

295   camera deployments. Samples sizes were low, but the community seems comparable to that in

296   the reference areas at the same time. It seems likely that the scavengers were attracted from a

297   larger area that could have included the proximate reference or undisturbed areas as suggested by

298   the similar arrival times of the scavengers in reference and disturbance deployments. This could

299   occur even if these animals were not commonly residing in the disturbance area due to habitat or

300   prey community alteration because the DISCOL experiment created a patchwork of habitats over

301   a scale as small as 10's of meters (Fig. 1).

302   The fish community remains affected by the DISCOL experiment even after 26 years.

303   Total fish density in the ploughed habitat of the DEA increased over time and in relation to the

304   reference and undisturbed habitat suggesting recovery. It should be noted that large interannual

305   changes were evident at the reference site with fish densities peaking 3 years post disturbance

306   and at high levels again at 26 years (Fig. 5). An increase in megafaunal density over the first 7

307   years of the experiment was already documented and hypothesized to be the result of increased

308   phytodetrital food flux and growing populations regionally (Bluhm, 2001). Such variation in

309   megafaunal abundance is a regular feature of abyssal communities (Kuhnz et al., 2014;Ruhl and

310   Smith, 2004). Comparisons between habitats at a point in time can provide a more robust means

311   to assess recovery after plough disturbance (Miljutin et al., 2011). We found no differences in

312   total fish density between the disturbed and undisturbed habitats at 26 years. Further, diversity

313   (ES 26) was slightly higher in the disturbed habitat areas, although with relatively small sample

314   sizes. However, the most common fish *I. meadi*, that makes up more than half of all the fish

315   observations, had only a third of the density in 26-year-old plough tracks compared to

316   undisturbed and reference areas, and only one individual was seen in the fresh EBS tracks (Fig.

317   4). This fish is found in the undisturbed habitat which occurs in a patchwork with the disturbance

318   tracks, hence regional reductions in population density are unlikely. Rather it seems that *I.

319   meadi* actively avoids the plough tracks, showing that even the mobile fish community remains

320   affected by the disturbance after more than two decades. This species' response likely relates to

321   its biology as a rather sedentary, small benthic fish that, based on limited data, feeds on

polychaetes, small bivalves, and crustaceans (Nielsen, 1966;Crabtree et al., 1991). Its prey may not have recovered in the tracks (Jones et al., 2017;Borowski, 2001). Most of the other fishes observed are benthopelagic and when swimming across a habitat mosaic might as easily be seen over an old plough track as over other habitat. Even if benthopelagic species tend to favor undisturbed habitat, this would be difficult to see in data at such a small scale. Our other benthic species include the lizardfish *B. mollis* which preys on mobile fishes and shrimps and *B. sewelli*, which is a larger member of the Ipnopidae, but was too infrequently observed to assess habitat preferences (Table 1).

Conclusions about fish community recovery over time must be taken with caution. With a sparsely distributed fauna and the high variability in density, there are limits on statistical power and thus our confidence. The earlier DISCOL surveys differed in methodology to the current surveys including average altitude of the camera above bottom, image quality, and attention to the fishes. Our diversity estimates may well be higher as a result. Density estimates could also be affected by these same factors. The most common fish in the surveys, *I. meadi*, is relatively small and despite reflective eyes (Fig. 2) may have been more visible in our 2015 surveys in closer proximity to the seafloor. The influence many of these parameters have had on abundance estimations of fauna in the DISCOL region has been investigated in detail for a region of the DEA which was surveyed several times during the initial 7-year period and again in 2015. In 2015, the OFOS was deployed at 1.7 and 4 m in this region, and additionally an AUV was flown at 5 m to image the same region of seafloor. The results from these comparative studies (Purser et al. submitted for this special issue) show the sensitivity of density and diversity indices in the DISCOL area to changes in flight height, illumination, and camera type. Larger megafauna, such as fish, were clearly visible in images collected from higher altitudes, therefore resulting in both higher diversity and abundance estimates for a given transect length than achieved with lower flying camera systems. Certainly, methodology plays a very important role in determining the accuracy of sampling strategies in this ecosystem for determination of these parameters.

Our results add to a growing body of literature that generally finds little or partial recovery of faunal communities, even decades after simulated mining disturbances. Epifaunal megafauna density was considerably lower in disturbance tracks made 20 and 37 years prior to re-survey during the OMCO experiment in the CCZ (Vanreusel et al., 2016). Meta-analyses of abyssal disturbance experiments in the CCZ suggest that recovery of density and diversity is

353 faster in mobile than sedentary fauna (Gollner et al., 2017;Jones et al., 2017). For instance, the

354 mobile holothurian community appears to have recovered from disturbance in terms of density

355 and community composition at the DISCOL site after 26 years (Stratmann et al., 2018). Most

356 holothurians are detrital deposit feeders and their food source settling from above may not be

357 greatly affected by the plough disturbance, whereas some fishes, such as *I. meadi*, likely rely

358 upon epifaunal and infaunal macrofauna for food. The meiofauna and macrofauna have not

359 recovered completely after 26 years in the CCZ (Miljutin et al., 2011), or after 7 years at the

360 DISCOL site (Borowski, 2001). Some of the variation in the recovery potential observed

361 between studies is undoubtedly derived from the variation in disturbance type and intensity. The

362 direct benthic scale of actual nodule mining activities is suggested to be from 300-600 $km^2 \, y^{-1}$

363 for a single mining license (Oebius et al., 2001;Levin et al., 2016). While it may seem that a

364 local disruption in *I. meadi*'s distribution is a mild fish community effect 26 years post

365 disturbance, it must be kept in mind that the DISCOL experiment did not completely disturb the

366 DEA and that the scale of this experiment is very small in relation to industrial scale deep-sea

367 mining. We argue that at industrial scales of seafloor disturbance, *I. meadi* could exhibit major

368 regional reductions in population density that would last for decades and such effects could

369 extend to other species as well. Fishes may avoid direct mining activities but experience long

370 term habitat losses at spatial scales that seem very likely to result in regional population

371 consequences. Plumes of sediment from collectors or from discharge of the ore dewatering

372 plume (Rolinski et al., 2001) will greatly expand this area and magnitude of effect. Therefore, it

373 seems unlikely that the small-scale disturbance experiments, such as DISCOL (~10.8 km^2), will

374 be adequate for evaluating the potential effects of full scale nodule mining. Further, the physical

375 disturbance made in all experimental studies to date have not been directly reminiscent of the

376 impacts actual mining will make in terms of volumes of surface sediment removed or displaced,

377 subsequent sediment compaction, or generation of the high resolution topographical changes

378 associated with the ridges and troughs likely to result from tracked mining vehicle movement

379 (Jones et al., 2017;Doya et al., 2017;Jones et al., 2018).

380

381 *4.3 Comparison of the DISCOL fish and scavenger communities to those within the CCZ*

382 Nodule mining is likely to affect very large areas of the seafloor over decades (Wedding

383 et al., 2015). Mobile fishes and other scavengers likely have the greatest ability to migrate away

384 from mining disturbances, but they may be affected regionally through the redistribution of prey

385 resources and sublethal effects from toxic metals or sediment plumes. Consequently, the

386 biogeographies of taxa, even mobile species, are an important input to spatial management

387 approaches (Watling et al., 2013). The scale of species distributions will help determine where

388 and how large reserve areas should be in order to protect species. Comparison of the present

389 findings in the south Pacific to those in the CCZ polymetallic nodule province to the north,

390 across the equatorial upwelling, provide some insight into the ranges of abyssal fishes and

391 scavengers in this mining relevant region. Past studies frequently combined fish and scavenger

392 taxa into larger functional groups such as megafauna (Jones et al., 2017), but some studies have

393 presented lists of species, which are the focus of the comparison here.

394   A number of the fish taxa observed with camera transects in the CCZ (Pawson and Foell,

395 1983;Radziejewska and Stoyanova, 2000;Tilot, 2006;Amon et al., 2017) have also been

396 identified in the DISCOL area suggesting large species distributions (Table 3). 10 of the 14 taxa

397 in the DISCOL region are shared with the CCZ. Four taxa were identified from DISCOL that

398 were not previously identified from the CCZ region, none of which were abundant. Four fishes

399 were observed in the various CCZ studies but not at the DISCOL site. A number of abyssal

400 species have pan-Pacific and even global distributions (Priede, 2017). However, we are not

401 suggesting that there is only a single community of fishes and scavengers integrated over 1000's

402 of kilometers. Rather it is likely that there are some species from this community, such as those

403 that occur in both the DISCOL and CCZ regions, with broad distributions that could recolonize a

404 mining license area if extirpated by mining. The extent of such conclusions must be made with

405 caution because the overlap between the two areas may be artificially high. Unrealistic overlap

406 could arise due to the difficulty in identifying species from photographs, particularly those taken

407 from high altitudes, and hence the use of genera and higher taxonomic categories. Further there

408 are some taxa which can easily be confused depending upon image quality. For instance in the

409 DISCOL site we identified the ophidiid, *Porogadus* sp. which has a long whip like tail and

410 narrow body similar to Halosaurs which have been observed in the CCZ (Amon et al., 2017) and

411 in an earlier study at the DISCOL site (Bluhm, 1994). We suspect that with increasing camera

412 resolution and better taxonomic experience, photographic data and its analysis will improve

413 greatly. Also, taxa are much more easily identified in oblique imagery. For instance, Halosaurs

414 have prominent high pectoral fins and a single short dorsal whereas *Porogadus* has a long low

dorsal fin all of which are seen in oblique imagery. We suggest the use of both oblique and vertical cameras on the same platforms in future studies. There has been some suggestion that oblique imagery would also alleviate avoidance issues with mobile taxa, but in the one abyssal study that used both oblique and vertical cameras, greater fish density was found in the vertical imagery (Milligan et al., 2016). Finally, collecting physical specimens and genetic data would be a great complement to the camera-based approach. Trawling for fish samples in mining claim areas will be challenging due to the great depth and the abundance of nodules, which can break nets and greatly damage specimens. Baited traps are effective for some of the fauna (Leitner et al., 2017;Linley et al., 2016).

The scavenging communities exhibit some interesting differences to those described from the eastern CCZ region and other abyssal Pacific locations. The dominant DISCOL scavengers were the shrimp *H. nereus*, eelpouts *Pachycara* spp., and the hermit crab *P. mirabilis*. The presence of large numbers of hermit crabs at the DISCOL site has been noted in earlier transect studies (Bluhm, 2001), and their large contribution to the scavenging community seems unique amongst abyssal scavenger studies. The most similar finding was a few hermit crabs (*Sympagurus birkenroadi*, MaxN= 2) attending bait from 2000 – 3000m depths off Hawaii (Yeh and Drazen, 2009). The large numbers of *H. nereus* is similar to the community in the eastern CCZ (Leitner et al., 2017). However, the eastern CCZ fishes were dominated by *Coryphaenoides* spp., which were not abundant at the DISCOL site. Overall the DISCOL scavenging community appears more similar to that observed in the western CCZ, which hosted lower numbers of *Coryphaenoides* spp. and greater numbers of ophidiids and shrimp (Leitner et al., 2017). The differences from east to west in the CCZ have been postulated to be related to the lower surface productivity in the west. Indeed, more oligotrophic regions have been shown to shift the dominance of the scavenging fishes from Macrourids to Ophidiids (Linley et al., 2017;Fleury and Drazen, 2013). However, the average long-term chlorophyll concentration at the DISCOL site estimated from the MODIS satellite (30x30km box from 2006-2016) is about 1.5 times higher (0.22 mg chl-a m^{-3}) than that reported by Leitner et al (2017) in the eastern CCZ. Whether the community differences observed between the DISCOL and CCZ regions are the result of variations in overlying productivity, species distributions, or other habitat factors cannot be discerned until a greater number of baited camera studies are conducted across the region.

446

In conclusion, the DISCOL site has a relatively diverse abyssal fish community dominated by *Ipnops meadi*. Fish density increased in the ploughed habitat type over time and became similar to undisturbed habitat types at 26 years post disturbance, but the density of *I. meadi* is still only a third of the undisturbed habitat types indicating that the DISCOL experiment continues to affect the fish fauna through altered distributions. At the temporal and spatial scales of industrial mining, changes in habitat availability could lead to population reductions even if fishes can avoid the direct activities of mining. The abyssal fish communities observed in the central eastern Pacific at DISCOL and the more northerly CCZ are similar with many shared taxa. However, further species level identifications are required which requires the collection of physical specimens through trawling or baited traps. The scavenging community in the DISCOL site is unique in the prevalence of the hermit crab, *P. mirabilis*, which does not appear in the CCZ in either camera transects or baited camera deployments. Not surprisingly, fishes and mobile scavengers appear generally to have large ranges but also large shifts in community composition across the CCZ (Leitner et al., 2017) and across the equator. As commercial mining of polymetallic nodule provinces rapidly progresses, with commercial field trials commencing in the Belgian and German claim areas of the CCZ in the first months of 2019, gaining a better understanding of these remote ecosystems is of paramount importance. Until key fauna, such as the various benthic fish species utilizing these habitats are better known, ensuring that appropriate management plans are developed to best minimize human impact during mining will be extremely problematic.

5. Data Availability

All OFOS images and data collected during the RV Sonne So242/2 cruise analyzed for this study are available with open access from the PANGAEA data repository: https://doi.pangaea.de/10.1594/PANGAEA.890634. Baited camera imagery is available through the BIIGLE data repository at https://annotate.geomar.de.

6. Author Contributions

JCD and ABL analyzed the data and wrote the manuscript. SM annotated the baited camera images and assembled the data. AP and YM designed and conducted the camera transect

477 experiments, quantified image coverage, helped write the manuscript, and generated the map

478 figure. JG digitized and archived the original baited camera images. All authors read and

479 commented on the manuscript.

480

481 **7. Competing interests**

482 The authors declare that they have no conflict of interest.

483

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650 **Table 1**. Numbers of photo transect (OFOS system) observations (all images/ timed images

651 only) for fishes in the DISCOL area by habitat type 26 years after initial experiment. The percent

652 of images with fishes are calculated from the timed images only.

OTU	Family	total	reference	undisturbed	transition	ploughed	ebs
				Habitat type			
Bathysaurus mollis	Bathysauridae	13/11	2/1	5/4	2	2	2
Bathytyphlops cf *sewelli*	Ipnopidae	5	0	3/3	0	2	0
Ipnops cf *meadi*	Ipnopidae	188/178	68/64	97/91	11	11	1
Liparidae	Liparidae	4/3	1	3/2	0	0	0
Coryphaenoides armatus/yaquinae	Macrouridae	6/5	0	3/3	3/2	0	0
Coryphaenoides leptolepis?	Macrouridae	1/0	0	1/0	0	0	0
Bassozetus cf *nasus*	Ophidiidae	6	2	1	2	1	
Bassozetus sp. B	Ophidiidae	2	0	1	1	0	0
Bathyonus caudalis	Ophidiidae	30/26	8	15/12	2	3/2	2
Leucicorus sp.	Ophidiidae	3/2	3/2	0	0	0	0
Ophidiid sp. 3	Ophidiidae	6	1	2	1	2	0
Ophidiidae unided	Ophidiidae	16/14	2	8/6	1	5	0
Porogadus sp.	Ophidiidae	11	4	3	3	1	0
Pachycara spp.	Zoarcidae	4/2	2/1	2/1	0	0	0
unidentified fish		11/10	4/3	4	0	2	1
	#fish	306/281	97/89	148/133	26/25	29/28	6
	# OTUs	14	10	13/12	9	8	3
	# images	16733	5964	7155	1209	2055	350
	# images with fish	300/275	97/89	145/130	23/22	29/28	6
	% images with fish	1.6%	1.5%	1.8%	1.8%	1.4%	1.7%

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Table 2. Deployment MaxN for each bait-attending species by camera deployment (FBOS system). DEA – DISCOL experimental area, *deployment filmed a plough harrow track.

Deployment	FBOS003	FBOS004	FBOS005	FBOS006*	FBOS007	FBOS013	average
Date	2/20/1989	3/3/1989	3/16/1989	3/21/1989	3/22/1989	2/16/1992	
Image interval (min)	5.5	3.5	5	2	3.5	3.5	
# images	729	791	681	683	718	734	724±43
Latitude	7° 2.12' S	7° 1.97' S	7° 4.83' S	7° 4.53' S	7° 4.55' S	7° 4.72' S	
Longitude	88° 26.53' W	88° 28.57' W	88° 21.33' W	88° 26.25' W	88° 27.92' W	88° 27.63' W	
General location	Reference area	Reference area	Reference area	DEA	DEA	DEA	
Depth (m)	4057	4167	4076	4220	4159	4170	
Fishes							
Barathrites iris	1	1		1	1		1
Bassozetus cf *nasus*	2	1		1		1	1
Coryphaenoides armatus/yaquinae	1	2	2	1	1	1	1
Leucicorus sp			1				1
Pachycara spp.	9	3	5	3	9	4	6
Synaphobranchidae	1	1	2		1	1	1
Crustaceans							
Hymenopeneus nereus	8	10	8	5	9	15	9
Total Penaeid shrimp	3	4	2	3	2	3	3
Cerataspis monstrosus	1	1		1	1		1
Benthiscymus sp.	2	2	1	2	1	2	2
Munnidopsis sp.		2	1			1	1
Munnopsidae	2	1	2	1	1		1
Mysidae		1	2	1			1
Probeebei mirabilis	1	9	4	3	4	6	5
Other taxa							
Octopoda	1		1				1
Ophiuroidea	1				1	1	1

657 **Table 3**. Fish taxa occurrences from DISCOL and abyssal sites of the CCZ. * listed in Bluhm

658 (1994), bc – observed by baited camera only, #only these taxa out of 17 are given in the original

659 reference

Taxa	Family	This study	(Amon et al., 2017;Amon et al., 2016)	(Pawson and Foell, 1983)	(Radziejewska and Stoyanova, 2000)	(Tilot, 2006)[#]
Bathysaurus mollis	Bathysauridae	x	x	x		x
Halosauridae	Halosauridae	*	x			
Bathytyphlops sewelli	Ipnopidae	x				
Ipnops meadi	Ipnopidae	x	x	x	x	x
Liparidae	Liparidae	x				x
Coryphaenoides armatus/yaquinae	Macrouridae	x	x	x	x	x
Coryphaenoides leptolepis?	Macrouridae	x				
Barathrites iris	Ophidiidae	bc	bc			x
Bassozetus sp.	Ophidiidae	x	x	x		
Bassozetus sp. B (sp 4 in Amon et al 2017)	Ophidiidae	x	x			
Bathyonus caudalis (sp 5 in Amon et al 2017)	Ophidiidae	x	x			
Leucicorus sp.	Ophidiidae	x				
Ophidiid sp. 1	Ophidiidae		x			
Ophidiid sp. 2	Ophidiidae		bc			
Ophidiid sp. 3	Ophidiidae	x	x			
Ophidiidae	Ophidiidae	x		x		x
Porogadus sp.	Ophidiidae	x				
Typhlonus nasus	Ophidiidae			x		x
Histiobranchus bathybius	Synaphobranchidae		x			
Synaphobranchidae	Synaphobranchidae	bc				x
Pachycara spp.	Zoarcidae	x	x			
Zoarcidae	Zoarcidae		x	x		

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Figure Captions

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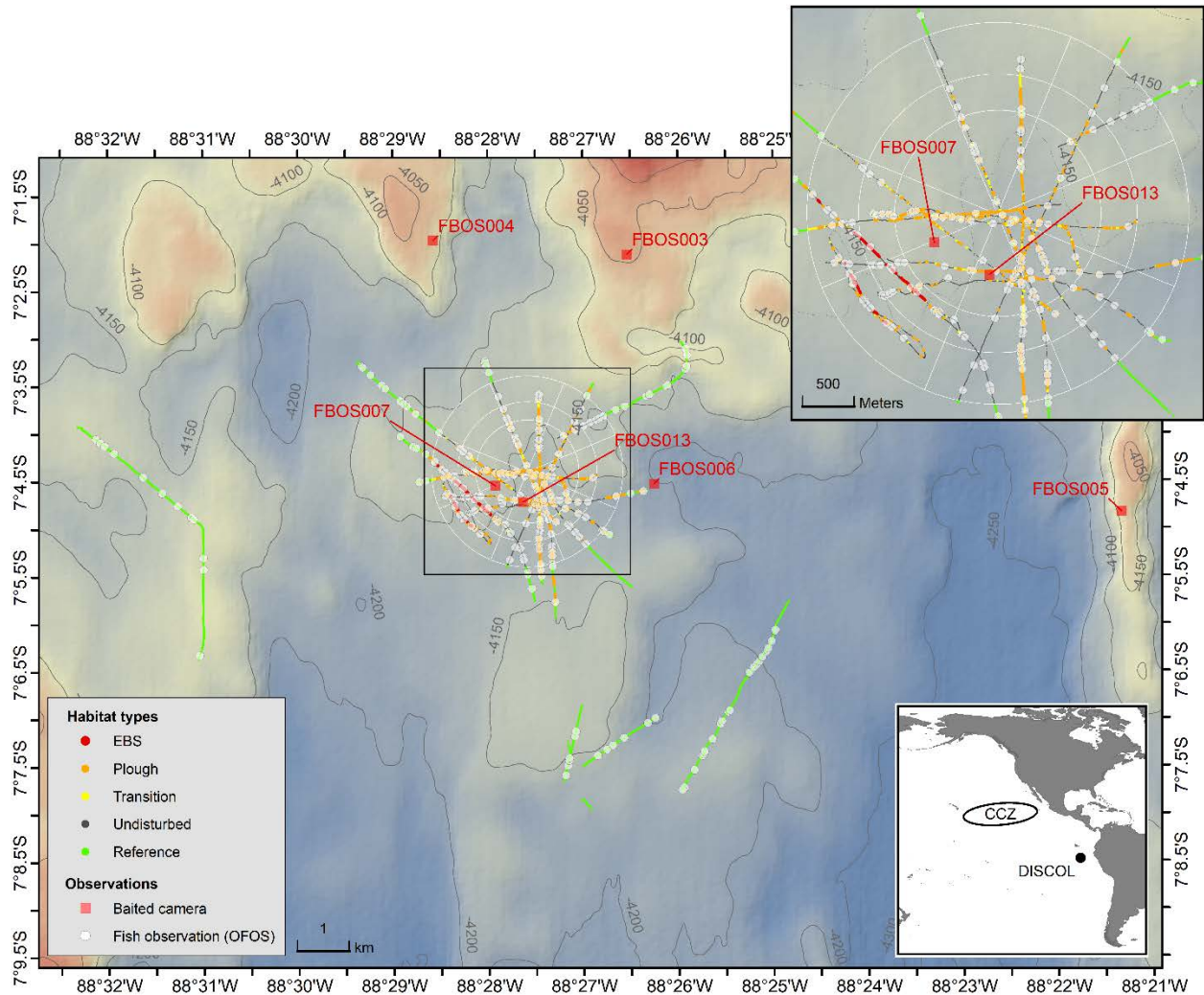
665
Figure 1. Map of the DISCOL study site showing the distribution of OFOS camera transects

666

667 (colors indicate the 5 habitat types), the OFOS-based fish observations (white circles), and the

668 location of the baited camera deployments (red squares). The white circular pattern and spokes

669 shows the location and extent of the DEA.

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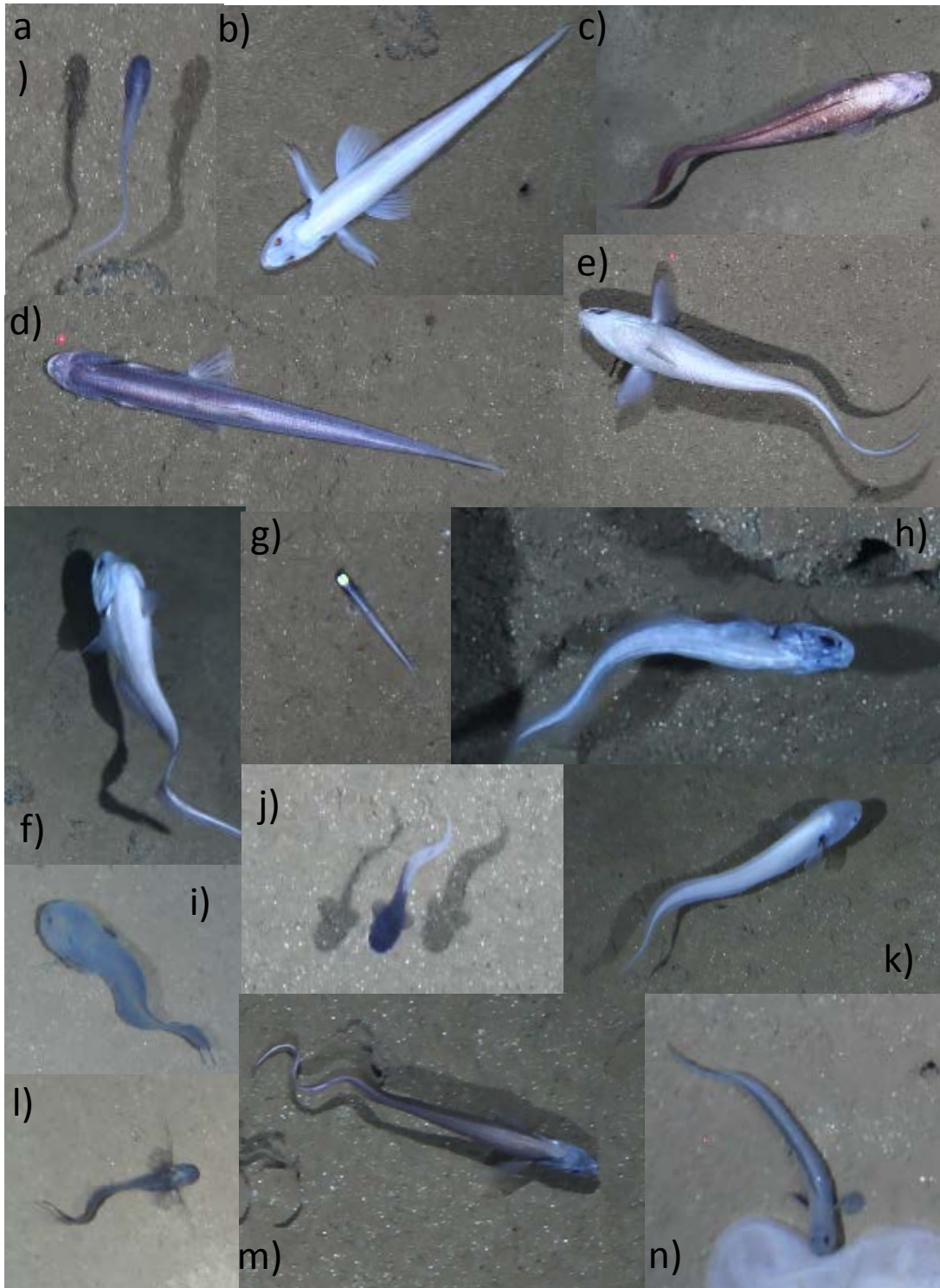

671
Figure 2. Representative images of OTUs identified in the DISCOL region during the 2015
survey. A) *Bassozetus* cf. *nasus* b) *Bathysaurus mollis* c) *Bathyonus* cf. *caudalis* d)
Bathytyphlops cf. *sewelli* e) *Coryphaenoides armatus*/*yaquinae* f) *Coryphaenoides leptolepis* g)

675   *Ipnops* cf. *meadi* h) *Leucicorus* sp. i) Liparidae grey morphotype h) Liparidae bicolor

676   morphotype k) *Bassozetus* sp. B l) Ophidiid sp. 3 m) *Porogadus* sp. n) *Pachycara* cf. *nazca*.

677

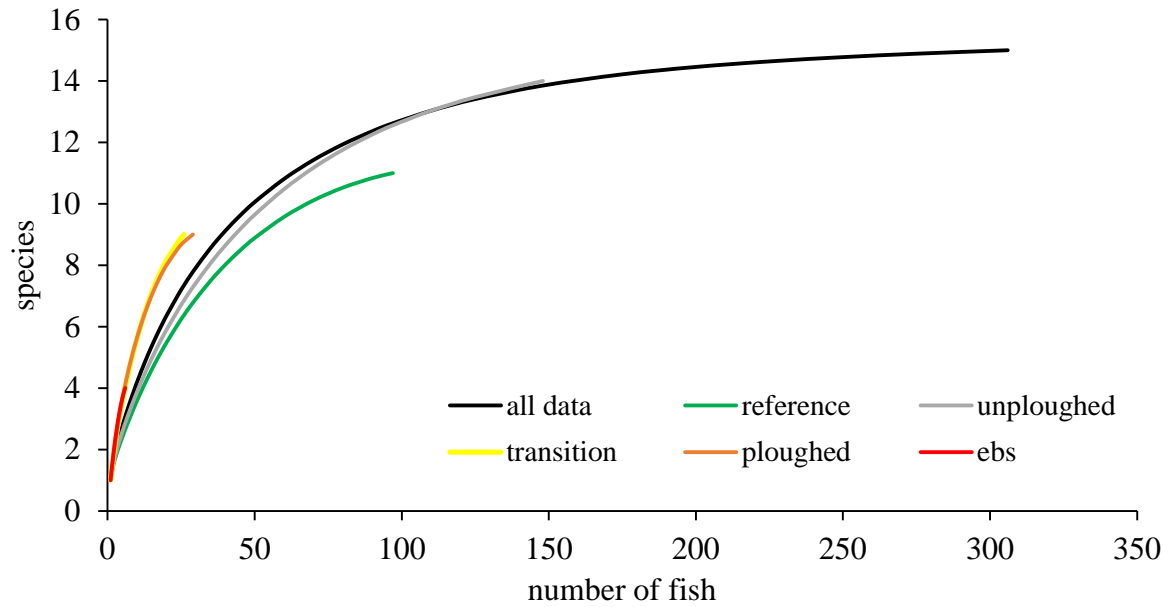



Figure 3. Rarefaction curves, estimated species richness as a function of the number of fish

observations, for OFOS transects across habitat types.

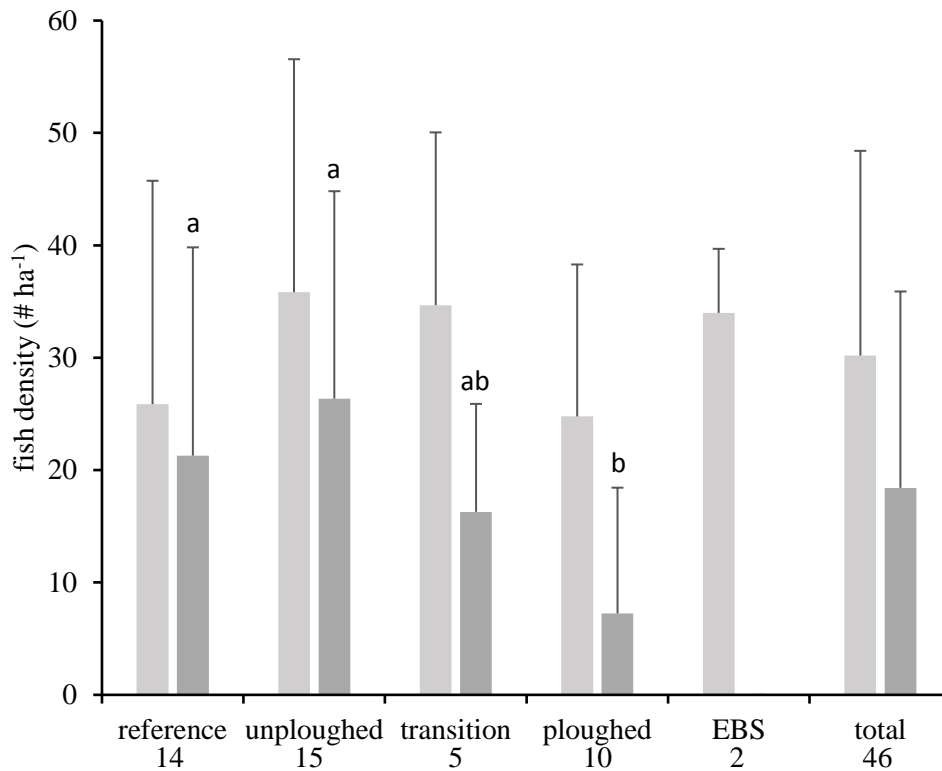
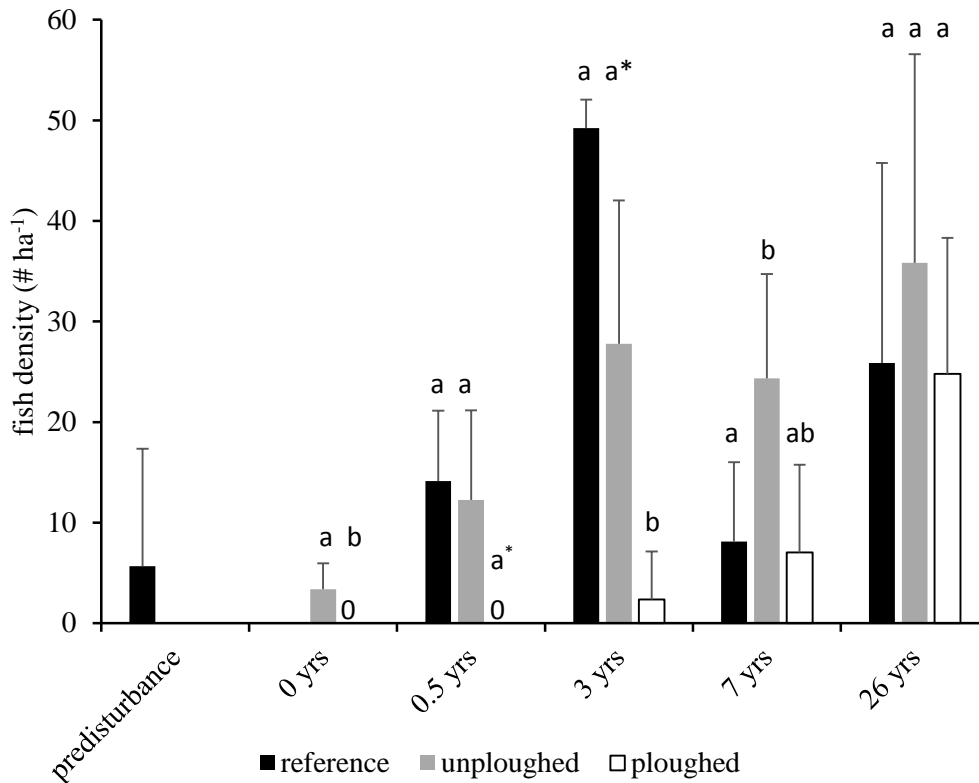



Figure 4. Total fish (light grey) and *I. meadi* (dark gray) density (mean and standard deviation)

from the 2015 OFOS transects by habitat type (timed images only) and for the entire dataset.

 The number of separate transects for each habitat type is given under its name. Letter symbols

687 for each habitat indicate significant differences in *I. meadi* density (p<0.05).

688

689
690 **Figure 5**. Fish density (mean and standard deviation) from predisturbance (1989) to 26 years

691 post disturbance (2015) in the reference area and in the ploughed and unploughed habitats of the

692 DEA. Data from predisturbance to 7 years post disturbance are from Bluhm (2001). Letter

693 symbols for each time indicate significant differences between habitat types (p<0.05). At 0.5 yrs

694 the asterisk indicates a marginal significant difference (p = 0.057).

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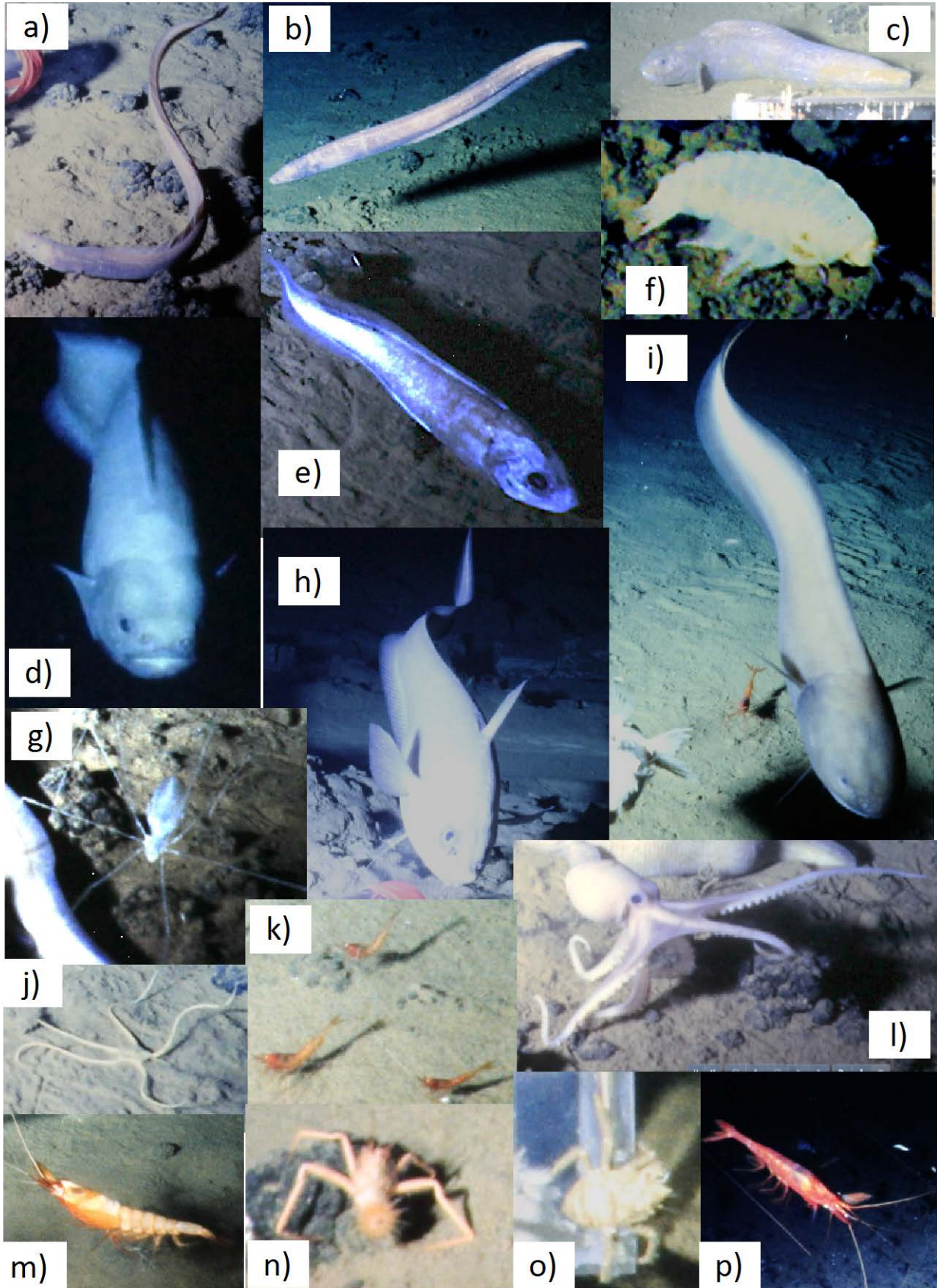
699 **Figure 6**. Representative images of OTUs identified using baited cameras in the DISCOL

700 region. Photos taken in 1989 and 1992. A) *Illypohis* sp. B) Synaphobranchidae C) *Pachycara*

701 *nazca* D) *Barathrites iris* E) *Leucicorus* sp. F) Large amphipod likely *Eurythenes* sp. G)

702 Munnopsidae H) *Coryphaenoides* sp. I) *Bassozetus* c.f. *nasus* J) Ophiuroidea K) *Hymenopeneus*

703 *nereus* L) Octopoda (*Vulcanoctopus* sp.) M) *Benthiscymus* sp. N) *Probeebei mirabilis* O)

704 *Munnidopsis* sp P) *Cerataspis monstrosus*

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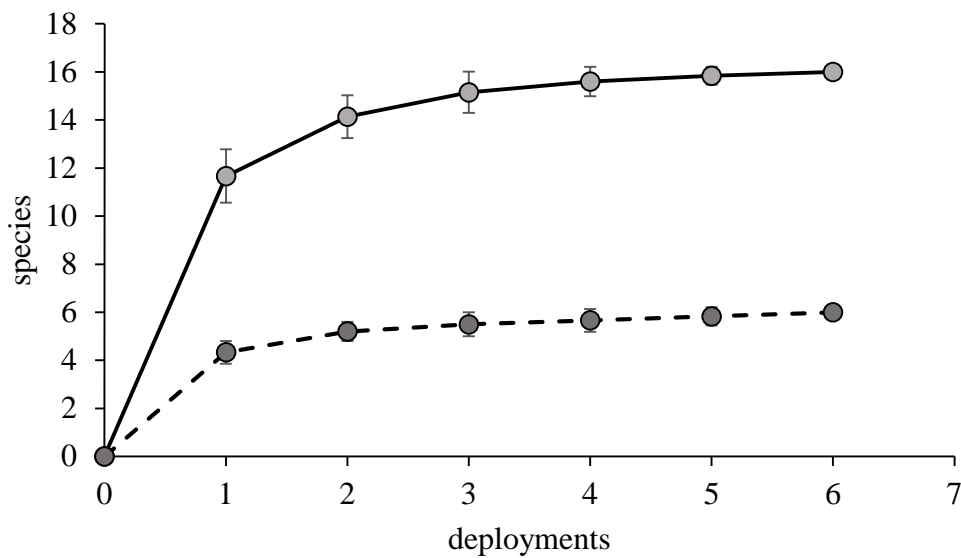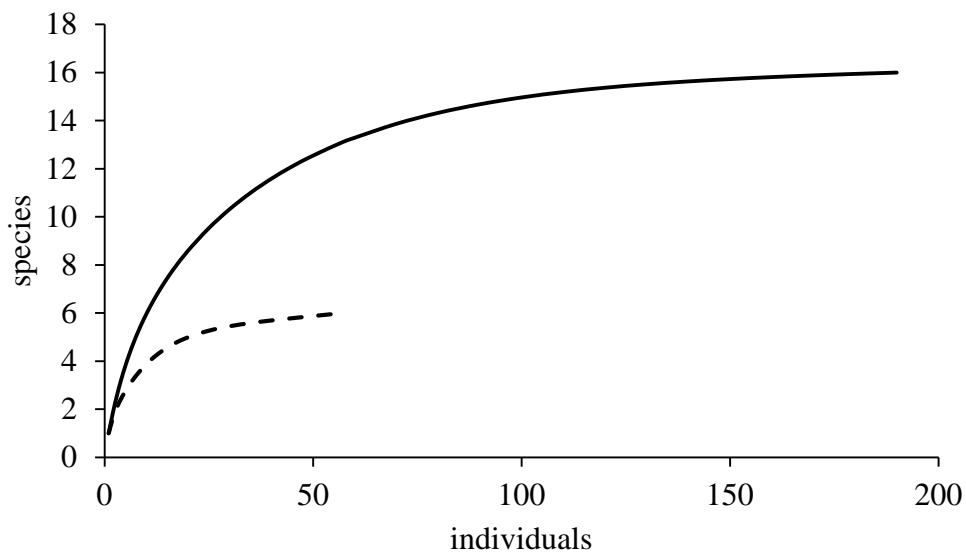
709

710 **Figure 7.** a) Rarefaction and b) species accumulation curves for baited camera observations.

711 Solid lines represent all data and dashed lines are fishes only (both based on MaxN data).